

Influence of forest structure and environmental variables on recruit survival and performance of two Mediterranean tree species (*Quercus faginea* L. and *Q. suber* Lam.)

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Abstract

We investigated the regeneration requirements of the two dominant tree species in a mixed-oak forest of SW Portugal: *Q. suber* (cork oak, evergreen) and *Q. faginea* (Portuguese oak, winter-deciduous). We hypothesized that: (1) recruits of different oak species are differentially influenced by soil and overstory variables; and (2) different factors explain the recruitment occurrence and performance of the same species. We sampled the recruits' height and diameter, and several environmental and forest structure variables of their microsites. Both recruitment occurrence and performance were modelled using generalized linear models. Our final models predicted the probability of occurrence of recruits of *Q. faginea* and *Q. suber* with 74% and 82% of accuracy, respectively, and explained about 50% of the variance of their recruitment performance. The recruits of *Q. faginea* tended to occur in microsites with higher canopy height, canopy density and litter cover, and closer to both conspecific and heterospecific adults, while the opposite was true for recruits of *Q. suber*. The performance of recruits of *Q. suber* was favoured by the higher litter cover (a good surrogate for N and P availability), but negatively affected by the higher litter depth. We concluded that: (1) there were significantly different regeneration niches for each species (*Q. faginea* and *Q. suber*), (2) the factors explaining the of recruitment occurrence differed from those explaining the recruitment performance; (3) the overstory plays a complex and important role in the regeneration process; (4) different variables apparently related with the same environmental factor (e.g. litter cover and litter depth) could affect recruits in an opposite way, (5) sensitive trade-offs must be considered for delineating management actions,

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4 35 since they could favour the regeneration of *Q. suber* but, at the same time, negatively
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6 36 affect the regeneration of *Q. faginea*.
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11 38 **Keywords:** Mediterranean forest, recruitment, evergreen oak, winter-deciduous oak,
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14 39 litter effects.
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17 41 **Introduction**

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21 42 The Mediterranean ecosystems have been recognized as one of the Earth's biodiversity
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23 43 hotspots (Myers *et al.* 2000). Nevertheless, natural forests throughout the Mediterranean
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25 44 Basin have been disturbed or destroyed by human activities, and nowadays they follow a
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27 45 fragmented distribution that occupies less than 10% of the area (Marchand
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29 46 1990). Therefore, it has been encouraged to look for a better understanding of the natural
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31 47 regeneration processes in Mediterranean forests (Acácio *et al.* 2007), because it is
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33 48 essential to know the ecological requirements for recruit establishment and growth,
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35 49 before trying to develop management and restoration strategies (Khurana and Singh
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37 50 2001). Besides, little is known about the natural regeneration of Mediterranean *Quercus*
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39 51 species, as long as a noticeable part of the research has been carried out in the dehesa
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41 52 (savannah-like) agrosystems (Pons and Pausas 2006).
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48 53 Evaluating the natural regeneration is an integrative way of evaluating the fitness and
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50 54 give an insight into the future of the populations under study (Pons and Pausas, 2006). As
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52 55 any plant species, the established trees in a Mediterranean forest have succeed in a chain
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54 56 of processes, including dispersion, germination and emergence responses, and seedling
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56 57 growth and survival (Herrera *et al.* 1994), but the regeneration requirements can be
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4 58 inferred from the micro-environmental conditions associated with the successful
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7 59 seedlings, saplings and juveniles of each species in their natural habitats (Marañón et al.
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9 60 2004).

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11 61 In this study we investigated the regeneration conditions of two *Quercus* species that
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13 62 frequently exhibit lack of regeneration (Pérez-Ramos and Marañón 2005, Estes-
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15 63 Martinez et al. 2006, Pausas et al. 2006, Acácio et al. 2007, Urbietta et al. 2008a, Urbietta
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17 64 et al. 2008b): the evergreen oak *Q. suber* L. (cork oak) and the winter-deciduous oak *Q.*
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19 65 *faginea* Lam. (Portuguese oak). These species occur mainly in the Mediterranean Basin
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21 66 (Tutin 1964), they are the dominant trees of mixed-oak Mediterranean forests on southern
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23 67 Portugal (Maltez-Mouro et al. 2005, García et al. 2006, Maltez-Mouro et al. 2007), and
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25 68 they are protected by the European Union Directives (Habitat Directive 92/43EEC).

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27 69 *Q. faginea* does not constitute mono-specific communities and, being together with
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29 70 other (tree and not tree) species, promotes the higher species richness of mixed-oak
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31 71 forests. However, and regardless its huge ecological importance, *Q. faginea* has not been
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33 72 much studied, compared to the high number of references for other species more useful
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35 73 directly for humans – as timber, fuel, charcoal, or resin extraction (Sánchez Arroyo
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37 74 2002). *Q. suber* is a tree species with socio-economic and cultural value, but very little is
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39 75 known about the recruitment and regeneration of this species (see review by Montero et
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41 76 al. 1994), and most of the research has been performed in the dehesa agrosystems. Even
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43 77 though, Pausas et al. (2006) have recently shown the lack of successful regeneration of *Q.*
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45 78 *suber*, and the need of land management to provide appropriate conditions for seedling or
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47 79 recruit establishment and growth. Therefore, studying the natural conditions prevailing in
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4 80 preserved forest patches with an adequate oak regeneration is of primordial importance
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6 81 (Khurana and Singh 2001, Acácio et al. 2007).
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9 82 The published literature on oak regeneration in Mediterranean forests gives important
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11 83 knowledge related with the processes of dispersion (e.g. Aparicio et al. 2008), seed
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13 84 predation (e.g. Pérez-Ramos and Marañón 2005), establishment (e.g. Lloret et al. 2004),
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15 85 and seedling survival and growth (e.g. Benayas et al. 2005, Antúnez et al 2001). Most
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17 86 studies on the first stages of regeneration of the Mediterranean oak species have been
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19 87 performed on seedlings growing under controlled conditions (Espelta et al. 1995; Quero
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21 88 et al. 2006, Sánchez-Gómez 2007). However, some studies carried out in natural
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23 89 ecosystems have shown that at low-light environments, the survival of seedlings of
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25 90 deciduous species (related with *Q. faginea*) exceeded the survival of seedlings of the
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27 91 evergreen *Q. suber* (Gómez-Aparicio et al. 2008). This pattern has been explained by the
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29 92 tendency of the deciduous species to be more frequent in habitats with denser overstory
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31 93 canopy, where the availability of water and nutrients is higher (Quero et al. 2006, Urbietta
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33 94 et al. 2008b).
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41 95 In this paper we aim to focus on the young and middle phases of the regeneration
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43 96 process in natural conditions. Therefore, we studied a natural Mediterranean mixed-oak
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45 97 forest and the oak recruits that have succeeded the first processes of regeneration, but still
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47 98 being part of the understory and suffering from the effects of the overstory (George and
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49 99 Bazzaz 1999, Maltez-Mouro et al. 2005). We analyze how several environmental factors
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51 100 related to the regeneration (occurrence and performance) success of *Q. suber* and *Q.*
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53 101 *faginea*, we evaluate the differences between them, and we investigate the role of the
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55 102 overstory structure and composition. We also show how a non-temporal approach can
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4 103 provide useful information on (still) well-preserved Mediterranean forests, which was
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6 104 urgent before any major change or disruption occurs - and as it is the case for many other
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9 105 endangered ecosystems.

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11 106 We hypothesized that: (1) in natural conditions, recruits of the two studied oak species
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14 107 are differentially influenced by different soil variables (litter depth, water content,
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16 108 nutrient availability) and by the overstory structure and composition; (2) different factors
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19 109 explain the recruitment occurrence and performance of the same species, because of
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21 110 changes in the regenerations niches along their ontogeny. We also relate our findings on
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24 111 natural conditions, with those described in other studies developed on controlled
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26 112 conditions.

27 28 29 113 30 31 114 **Methods**

32 33 115 ***Study site***

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36 116 The study site is located in the Sudoeste Alentejano e Costa Vicentina Natural Park,
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38 117 SW Portugal (37° 40' N, 8° 43' W). It is a mixed-oak forest composed of evergreen oaks
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41 118 (cork oak, *Q. suber*) and semideciduous oaks (Portuguese oak, *Q. faginea*), on a north-
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43 119 facing slope (32°). Other frequent woody species are the strawberry tree (*Arbutus unedo*
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46 120 L.), the laurestine (*Viburnum tinus* L.) and the kermes oak (*Quercus coccifera* L.) (see
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48 121 Maltez-Mouro et al. 2005).

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50 122 The climate is typically Mediterranean, with mild wet winters and warm dry summers.
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53 123 The mean annual precipitation is ca. 600mm, with only 10% occurring between May and
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55 124 September, and the mean annual temperature is ca. 15 °C, with mean maximum and
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58 125 minimum annual temperatures of ca. 29 °C and 6 °C, respectively (PNSACV 2002). Soils

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4 126 are acidic (mean pH=5.0) and low in nutrients (especially in N and P, see Maltez-Mouro
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6 127 et al. 2005).

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9 128 The studied forest site is within an area that has undergone a long history of fire and
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11 129 land use, but it is relatively well preserved, with no record of fire or logging since at least
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13 130 1956. Management is limited to the periodic (at approximately 9-year intervals) removal
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15 131 of the bark from the largest cork oak trees, for cork production. The oak regeneration is
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17 132 good, with frequent recruits (~ 0.2 individuals/m²) of the two dominant *Quercus* species
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19 133 (Maltez-Mouro et al. 2007).
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26 135 ***Study species***

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28 136 *Q. faginea* is a winter-deciduous medium high tree, which may reach only a high-shrub
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30 137 stature, due to human-caused conditioning or ecological limitations. However, and in
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32 138 contrast to other *Quercus* species, *Q. faginea* can produce seeds immediately when
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34 139 reaching the shrub phase (Sánchez Arroyo, 2002). The seeds are dispersed mainly by
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36 140 gravity near the mother tree, but they can be dispersed short-distance by rodents (Pulido
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38 141 and Díaz 2005), or long-distance by birds (Gómez 2003). It is a slow-growing species
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40 142 that propagates both by seeds and sprouting from trunks and roots, and the latter produces
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42 143 vegetative saplings that are difficult to distinguish from old seedlings.
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48 144 *Q. suber* is an evergreen tree rarely reaching 20 m height, and typical for its corky
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50 145 bark. Most cork oak trees occur in highly managed savannah-like agrosystems
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52 146 (designated “dehesas” or “montados”), but they also constitute rare and fragmented
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54 147 forests of south-western Iberian Peninsula. The dispersion strategies of this species are
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56 148 similar to those referred for *Q. faginea*.
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4 149 The two distinct regeneration strategies (vegetative sprouts and seedlings) may have
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6 150 different responses to water and nutrients, and sprouts usually show higher survival and
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9 151 growth rates than seedlings (Pardos et al. 2005). However, both strategies were put
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11 152 together in the present study, since the main objective was to determine the ability of a
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13 153 mixed-oak Mediterranean forest to (self-) maintain the floristic and ecological
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15 154 characteristics, and at what extent (and how) the overstory could influence the ecosystem
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17 155 dynamics, independently from the strategies used by each species. Seedlings and
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19 156 vegetative sprouts are hereafter named recruits.
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25 26 158 ***Sampling methods*** 27

28 159 We studied a forested slope of 70m length by carefully exploring two transects of 32 x
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30 160 10 m located in the upper- and lower-slope, respectively. Every young individual of *Q.*
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32 161 *faginea* and *Q. suber* between 10 and 130 cm height was censused.
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36 162 The recruits and the micro-environmental conditions of their habitat were sampled using
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38 163 plastic rings of 50 cm diameter centred in each one, for measuring (either on the forest
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40 164 floor inside the rings or within a vertical cylinder above them) the following micro-
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42 165 environmental and forest structure variables (units, classes, and sampling gear in
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44 166 brackets): soil moisture (% volume, using time domain reflectometry – TDR); slope
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46 167 (degrees, using a clinometer positioned on the floor); overstory canopy density (% using
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48 168 a spherical densiometer positioned 1m above the ground); litter ground-cover (% by
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50 169 direct visual estimation at increments of 5%), litter depth (cm); overlying species over
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52 170 each recruit (or the occurrence of canopy gaps); maximum overstory canopy height (six
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54 171 categories: 0, 1, 2, 4, 6, and 8 m); density of overstory canopy layers (counting one layer
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per each height class); distance to the nearest conspecific adult; and distance and the species name of the nearest adult of a different species (considering as an adult every plant able to reproduce).

For interpreting the observed environment-recruit relationships, we made use of a previous study (García et al. 2006) on data gathered in the same season and site, which included measurements of soil litter cover and N and P availability. According to their results, in our study we could assume that the litter cover and the overstory density were proxies for the nutrient (N,P) and light availability, respectively.

Data analysis

The statistical modelling of recruitment occurrence (i.e. presence/absence) of *Q. faginea* and *Q. suber* was performed using the generalized linear model (GLM), with binomial error and a logit link function. Akaike's information criterion (AIC) was used to select the best models, according to the Burnham and Anderson's (2002) criteria. The selected models were checked for overdispersion, residual patterns, and possible artefacts derived from extreme values (Dobson, 2002), before the final selection. The overall performance of the model fit for that dichotomous dependent variable, was expressed using the percent of success in predicting occurrence.

The recruitment performance was evaluated from the shoot number, diameter (calliper, at 10 cm) and height of each recruit. That is, we used the product between basal area (at 10 cm height) and height, as a surrogate of the recruit biomass for fitting the regression models described next. The dependent variable was modelled using the normal distribution of error. The overall goodness of fit of the model was expressed using the

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4 195 *R*²-statistics. When necessary, variables were transformed for skewness correction. The
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6 196 basic assumptions for residuals of the fitted models (i.e. normality and independence)
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9 197 were tested (using the Shapiro-Willk's and the runs tests, respectively) before the
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11 198 definitive models were selected.
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14 199 The non-parametric Mann-Whitney U-test was used to compare the average values of
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16 200 the microsite variables and the recruits' characteristics of *Q. faginea* and *Q. suber*. The
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18 201 overall relationships between the measured environmental variables (i.e. the structure of
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20 202 the micro-environmental data), was explored with principal component analysis (PCA).
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23 203 For controlling the increased proportion of "false positives" due to repeated testing,
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25 204 we applied an overall FDR correction at the 5% level, as suggested by García (2003,
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27 205 2004). Data analyses were performed using the Statistica (Statsoft, 2001) and the SPSS
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29 206 (SPSS Inc. 2004) software packages.
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35 208 **Results**

36 209 *Microsite environmental data*

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38 210 The PCA analysis of the microsite environmental data showed a strong underlying
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40 211 structure, since more than 50% of the total variance was extracted by only two underlying
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42 212 components (Table 1). The main component of variation (PCA1) accounted for about
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44 213 35% of the overall variance, and it could be interpreted as a gradient of increased
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46 214 overstory density (highly correlated to canopy density, number of canopy layers and
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48 215 maximum canopy height) and litter cover. This gradient summarized a tendency of the
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50 216 darker microsites to be richer in some key nutrients, as detected in previous studies
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52 217 (Maltez-Mouro et al. 2005, García et al. 2006).
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4 218 The second independent underlying gradient (PCA2) could be interpreted as a combined
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6 219 gradient of litter depth and soil moisture. Interestingly, litter cover and litter depth were
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9 220 related with different underlying components, the former closely related to the increased
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11 221 canopy density and the second to the increased soil moisture (Table 1).
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16 223 *Differences in the regeneration niche*
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19 224 A total of 93 recruits were sampled and used in the analysis: 55 belonging to *Q. suber*
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21 225 and 38 to *Q. faginea*. These two oak species that dominate in the overstory of the studied
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23 226 mixed-oak forest, but other large shrubs were also found and corresponded to their
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26 227 nearest heterospecific neighbours: *Arbutus unedo*, *Phyllirea angustifolia*, *Erica arborea*,
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28 228 *Quercus coccifera*, *Viburnum tinus* and *Rhamnus alaternus*.
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31 229 The average values and the results of the U-test comparing the variables measured for
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33 230 each species of recruits are shown in Table 2. These results showed that most of the
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35 231 recruits' characteristics (i.e. height, basal area and overall performance), most of the
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37 232 canopy density -related variables (canopy density and maximum canopy height), and the
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39 233 litter cover (but not litter depth), were significantly higher in the microsites where recruits
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41 234 of *Q. faginea* occurred. On the other hand, the distance to the closest adult of the same
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43 235 species, and their basal area was significantly higher for recruits of *Q. suber* (Table 2).
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50 237 *Modelling the recruitment occurrence and performance*
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53 238 Tables 3 and 4 summarize the fitted models that best explained the occurrence
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55 239 (presence/absence) and performance of recruits of the two studied species of *Quercus*.
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58 240 According to the results in Table 3, the microsites where those recruits were predicted to
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occur, are clearly contrasted in at least four variables: the canopy maximum height, the
 litter cover, the basal area of the nearest conspecific, and the distance to adults of another
 woody species. The model with these four predictors was able to predict the suitable
 microsites for *Q. faginea* and *Q. suber*, with an accuracy of 74% and 82%, respectively.
 The recruits of *Q. faginea* had higher probability of occurrence in microsites with higher
 canopy height and litter cover, and further from big heterospecific adults, as well as their
 nearest conspecific adults were thinner. At the opposite, the recruits of *Q. suber* tended to
 occur in microsites with lower canopy and litter covers and closer from heterospecific
 trees, and they had bigger nearest conspecifics.
 The models predicting recruitment performance (Table 4) explained 47% and 50% of the
 variance of recruits of *Q. faginea* and *Q. suber*, respectively (Fig. 1), and the assumptions
 for residuals were met (Fig. 2). The results in Table 4 showed that the factors affecting
 recruitment performance differed from those affecting recruitment occurrence, for the
 two studied species: for *Q. faginea*, no matches were found; for *Q. suber*, litter cover had
 significant opposite effects on recruitment occurrence and performance (i.e. the higher
 litter cover was associated with an increased performance, but also with a lower
 recruitment occurrence). Besides, different variables related with the same environmental
 factor, affected the recruits in a different way: the performance of recruits of *Q. suber*
 was favoured by higher litter cover, but negatively affected by higher litter depth (Table
 4). In fact, although those two different variables for litter abundance (cover and depth)
 were slightly correlated, they shared only 14% of their variance. That is, they behaved as
 opposite environmental factors conditioning the recruitment performance of *Q. suber*.

Discussion

Our study showed that the effects of the community structure and environmental variables on the recruitment of *Q. suber* and *Q. faginea* are complex (Fig. 3). Besides, our results showed that the requirements for recruitment occurrence and recruitment performance differed. This could be explained by the changes in the regeneration niches of different tree species along their ontogeny, as it has been remarked in other studies (Cavender-Bares and Bazzaz 2000, Medavilla and Escudero 2004, Quero *et al.* 2008).

The recruits of *Q. faginea* tended to occur in microsites with higher canopy density and height and higher litter cover, compared with microsites occupied by recruits of *Q. suber*. These results are consistent with different studies in Mediterranean environments, which have suggested that the seedling survival of a winter-deciduous species (*Q. canariensis*) exceeded the survival of the evergreen *Q. suber*, in low-light environments (Gómez-Aparicio *et al.* 2008). On the other hand, García *et al.* (2006) have shown a strong relationship between the litter cover and the overstory cover, and between the litter cover and the concentration of available P and available N, in the topsoil of the same studied forest. Therefore, recruits of the winter-deciduous *Q. faginea* could take advantage of their shade tolerance (Sánchez Arroyo 2002, Benayas *et al.* 2005) to benefit from the higher availability of the two main limiting soil nutrients, because they grow faster (Reich *et al.* 1992, Antúnez *et al.* 2001), and have a higher efficiency in the assimilation of energy and carbon dioxide (Wright *et al.* 2004). Other authors have also shown that the deciduous species of *Quercus* tend to be more abundant than the coexisting evergreen species of *Quercus*, in habitats having higher water, higher nutrient availability, and denser overstory canopies (Quero *et al.* 2006, Urbietta *et al.* 2008b).

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4 287 Regarding the recruitment performance, the multi-layered canopy had a positive effect
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6 288 on *Q. faginea*, but the favourable multi-layered canopy could not be associated with the
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9 289 extremely dense canopies covers, which reduced recruitment performance of *Q. faginea*.
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11 290 It also showed to be an important factor for the existence of suitable light supplies: the
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14 291 higher number of canopy layers was strongly correlated with the main gradient of
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16 292 overstory density (Table 1). It has been shown that some degree of canopy closure
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19 293 corresponds to a moderate radiation that can ameliorate (or, at least, not aggravate) the
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21 294 drought impact on oak seedlings during summer, and thus may be crucial for recruitment
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24 295 (Quero et al. 2006, Puerta-Piñero et al. 2007). High levels of radiation usually lead to
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26 296 increased temperatures and higher water evaporation rates, exerting a negative effect on
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29 297 oak seedlings (Valladares et al. 2000). In fact, the recruits exposition to high irradiance
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31 298 and water losses during the harsh (hot and dry) summer, are the major causes of seedling
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34 299 mortality of Mediterranean woody species (Herrera et al. 1994). The leaf behaviour of the
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36 300 studied species could explain our results, since it is related with the species strategies for
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38 301 responding to drought (Quero et al. 2006): the winter-deciduous oak species (*Q. faginea*)
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41 302 could be expected to be more dependent from the canopy cover than the evergreen
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43 303 species (*Q. suber*), which is able of better tolerating summer stress (Mediavilla et al.
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46 304 2004, Quero et al. 2006, Sanz-Pérez et al. 2007, Urbieto et al. 2008b).

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48 305 The average litter cover was significantly lower for the recruits of *Q. suber*, compared
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51 306 with the recruits of *Q. faginea*, as well as the microsites with high litter cover percentages
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53 307 had a significantly lower probability of occurrence of recruits of *Q. suber*. However,
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55 308 considering only the range of litter covers occupied by *Q. suber*, a significant positive
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58 309 effect of litter cover on recruit performance was observed. Rinkes and McCarthy (2007)

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4 310 recently reported that an adequate litter cover was needed to promote oak seedling
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6 311 establishment, and our results showed that the nutrient enrichment associated with litter
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9 312 accumulation (García et al. 2006) was also an advantage for this species, when it was not
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11 313 associated with strong light limitations nor increased litter depth. Sánchez-Arroyo (2002)
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14 314 has also reported an association between soil richness and higher regeneration rates,
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16 315 together with high canopy densities that preserved recruits from insolation, in a north-
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19 316 faced slope occupied by deciduous trees that produced high amounts of litter.

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21 317 On the other hand, we detected a significant negative effect of the higher litter depth on
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23 318 recruitment performance of *Q. suber*. Some authors explained these negative effects as a
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26 319 result of the mechanical and/or chemical effects of litter (e.g. Facelly and Picket 1991),
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29 320 and Maltez-Mouro et al. (2007) have shown that unlike the recruits of *Q. suber*, the
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31 321 recruits of the winter-deciduous species *Q. faginea* are able to tolerate the thicker litter
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33 322 layers, which are mostly produced by their conspecific adults. Again, the deciduous
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36 323 behaviour of *Q. faginea*'s leaves showed to play an important role in the community
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39 324 structure and dynamics (Sánchez-Arroyo 2002).

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41 325 The recruits of *Q. suber* tended to occur in microsites farther from conspecific adults.
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43 326 Other studies have shown that the distance between recruits and conspecific adults can be
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46 327 a major factor determining the recruitment spatial patterns (Maltez-Mouro et al. 2007)
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49 328 and partially reflects the dependence of recruits on their mother trees and dispersion
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51 329 strategies (Herrera et al. 1994). The basal area of the closest conspecific adult was
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53 330 significantly higher for recruits of *Q. suber*, as well as the fitted model suggested a higher
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56 331 probability of occurrence of recruits of this species in microsites located in the nearby of
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58 332 adults with higher basal area. Two reasons contribute to explaining these results. First, *Q.*

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4 333 *faginea* can produce seeds in the shrub phase, while the trees of *Q. suber* need to be
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6 334 larger to produce seeds (Sánchez Arroyo 2002). Second, the recruits of *Q. faginea* need
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9 335 or tolerate shade in their first years of living (Sánchez Gómez 2007), while *Q. suber* may
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11 336 be considered an “intermediate” species, i.e. it is a transition species between winter-
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14 337 deciduous and other evergreen Mediterranean oaks (i.e. *Q. faginea* and *Q. ilex* L.,
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16 338 respectively) with respect to leaf longevity and drought tolerance (David et al. 2007), and
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19 339 thus it needs and tolerates shaded environments but only when drought and competition
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21 340 for water are not much severe (Benayas et al. 2005).

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23 341 The performance of recruits of the two studied species was significantly increased
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25 342 farther from conspecific adults. This could be explained by the higher competition for
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28 343 light and/or water in microsites near conspecific adults. In contrast, the recruitment
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30
31 344 performance of each studied species was affected in a different way by the heterospecific
32
33 345 adults: the recruits of *Q. suber* were not affected by the proximity of any heterospecific
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35
36 346 adult, while the recruits of *Q. faginea* were strongly affected in the nearby of two
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38
39 347 evergreen arborescent shrub species - *Viburnum tinus* and *Q. coccifera*. The negative
40
41 348 effect of *Q. coccifera* on recruits of *Q. faginea* is probably because the former is known
42
43
44 349 to be a strong competitor for water, specially during the dry season (Castro-Diez et al,
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46 350 2007). More studies would be necessary to evaluate how the adults of *V. tinus* play the
47
48
49 351 detected negative influence on recruits of *Q. faginea*, and why recruits of *Q. suber* go
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51 352 beyond both influences.

52
53 353 Maltez-Mouro et al. (2007) have shown that the higher soil moisture positively
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55 354 correlated with the occurrence of seedlings of the two studied species of *Quercus*. Other
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58 355 studies have also shown that the canopy density, herbaceous ground-cover, or the litter
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amounts, are strongly related with the availability of water (e.g. Benayas et al. 2005, Maltez-Mouro et al. 2005). Moreover, it has been shown that the deciduous oak species are not so efficient as the evergreen oak species on relatively dry soils (Corcuera et al. 2002). However, in our study the soil moisture was not significantly different in microsites inhabited by recruits of *Q. faginea* or *Q. suber*, nor it was an important variable in explaining the recruitment occurrence/performance of these species. These unexpected results could be explained by: (1) the limited set of measurements of the water-content variable; (2) the superficial measurement (i.e. from upper soil horizons) of soil moisture – because oak seedlings depend from their deep rooting to surpass the summer drought (capturing water from the deeper soil horizons); (3) the existence of other significant and more predictable variables that correlated with soil water content – and thus gave to the latter an apparent lack of power in predicting regeneration. This was the case of the litter depth variable, which was statistically associated to the same underlying gradient (Table 1). Different studies have reported increased soil water contents with higher litter accumulation, but the corresponding effects on soil water dynamics have received scarce attention in forest ecosystems (Facelly and Pickett 1991).

Conclusions

In the studied mixed-oak Mediterranean forest, there were significantly different regeneration niches for each of the dominant species, *Q. faginea* and *Q. suber*. The effects of the community structure and environmental variables on recruitment were in agreement with the ecophysiological characteristics known for each species and for the related evergreen and deciduous species of *Quercus*. However, our study showed that the

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4 379 factors affecting the probability of recruitment occurrence differed from those affecting
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6 380 the recruitment performance. Also, those factors interacted in a complex and, to a great
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9 381 extent, unpredictable way, and different variables of to the same environmental factor
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11 382 could affect recruits in a very different (even opposite) way.
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14 383 The structural and environmental heterogeneity of the forest was shown to be extremely
15
16 384 important to promote the regeneration of the two dominant oak species, and the overstory
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18
19 385 structure and composition played an important role in the regeneration process. We
20
21 386 suggest that there is a huge risk of a negative feedback of some overstory species that
22
23 387 usually co-dominate in these forest types - in particular *Q. coccifera* and *V. tinus* - over
24
25 388 the dominant (*Quercus*) species trying to succeed in the understory (before reaching the
26
27 389 overstory layers). This could ultimately lead to a completely different forest composition
28
29 390 and structure, and the corresponding loss of diversity.
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33 391 The data gathered in this study, and the models fitted to the recruitment occurrence and
34
35 392 performance of *Q. suber* and *Q. faginea*, suggested that clearing practices would favour
36
37 393 the regeneration of *Q. suber*, while more closed canopies with deep litter layers would
38
39 394 favour *Q. faginea*. However, both an excessive cover of some shrub species and the
40
41 395 complete absence of woody canopies, would negatively affect the regeneration of *Q.*
42
43 396 *faginea*. Since there was no lack of regeneration of the two dominant oak species in the
44
45 397 studied forest site, our results are relevant for threatened Mediterranean forests with
46
47 398 serious regeneration problems. Knowing the ecological requirements and limitations of
48
49 399 the survival and performance of different oak species is essential, for developing
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51 400 ecologically –based management and restoration strategies for mixed-oak Mediterranean
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53 401 forests.
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Acknowledgements

This work was financially supported by the SFRH/BD/8322/2002 grant to the first author, given by the Portuguese Technology and Science Foundation, Ministry of Sciences and High Education. L.V.G. was supported by the projects HETEROMED (REN2002-4041-C02-02) and DINAMED (CGL2005-05830-C03-03/BOS) from the Spanish Ministry of Education and Science. Special thanks go to Ana Mouro for assisting in the fieldwork and to Teodoro Mara  n for comments and reviews of the ms.

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602

603 Table 1. Results of the PCA analysis of the measured micro-environmental predictors.

604 Factor loadings exceeding 0.5 (in absolute value) are in bold.

605

606 Table 2. Recruits' characteristics and microsite conditions. Means and standard

607 deviations of the measured variables are shown. The critical p -value for controlling the

608 False Discovery Rate at the 5% level throughout the study was 0.0354.

609

610 Table 3. Environmental factors that significantly explained the occurrence of *Q. faginea*

611 (1) or *Q. suber* (0) in the studied forest site. Data were modelled using a generalized

612 linear model with binomial error and a logit link. Abbreviations: dbhNCA, diameter at

613 breast height of the nearest conspecific adult; DNHA, distance to the nearest

614 heterospecific adult.

615

616 Table 4. Effects of the environmental factors on the recruitment performance of *Q.*

617 *faginea* and *Q. suber*. Data were modelled using a generalized linear model with normal

618 error. Abbreviations: DNCA, distance to the nearest conspecific adult; DNHA, distance

619 to the nearest heterospecific adult; NA, nearest adult; Qc, *Quercus coccifera* Vt,

620 *Viburnum tinus*.

621

622 Figure 1. Observed and predicted values of recruitment performance, expressed as \log_{10}

623 (basal area x height) of recruits of *Q. faginea* (a) and *Q. suber* (b). Multiple-R values for

624 the fitted models were 0.73 and 0.72, respectively.

625

626 Figure 2. Residuals and predicted values of the modelled performance (expressed as \log_{10}
627 (basal area x height)), for recruits of *Q. faginea* (a) and *Q. suber* (b). The assumptions of
628 normality and independence of the residuals were tested and verified with the Shapiro
629 Willk's ($p=0.05$ and 0.37 , respectively) and Runs tests ($p=0.29$ and 0.92 , respectively).

630

631 Figure 3. Diagram summarizing the effects of environmental and community structure
632 variables on the regeneration and performance of *Q. suber* and *Q. faginea*. Each rectangle
633 represents higher values of that variable. The solid and dotted lines represent positive and
634 negative effects of the variable, respectively.

Table

	PCA1	PCA2	PCA3
Canopy density	0.7	0.3	0.1
Canopy height	0.6	-0.2	0.4
Canopy layers	0.7	0.2	0.0
Litter cover	0.7	0	-0.4
Soil Hum	-0.2	-0.8	-0.1
Litter Depth	0.4	-0.6	-0.5
Slope	0.2	-0.5	0.7
Eigenvalues	2.2	1.3	1
Total variance (%)	31.7	18.7	14.9

Table

Variables	<i>Q. faginea</i>	<i>Q. suber</i>	<i>U</i>	<i>P</i>
<i>Recruit parameters</i>				
Shoot number	2.9 ± 2.9	1.8 ± 1.3	795.5	0.0509
Height (cm)	57.8 ± 34.1	39.1 ± 23.1	761.0	0.0098
Basal area (cm ²)	0.7 ± 0.8	0.4 ± 1.6	707.5	0.0079
Overall performance (cm ³)	56.8 ± 74	38.6 ± 208	688.5	0.0050
<i>Microsite parameters</i>				
Slope (°)	31.6 ± 8.0	29.2 ± 10.9	837.0	0.1051
Soil moisture (m ³ .m ⁻³)	0.1 ± 0.01	0.1 ± 0.02	653.5	0.1135
Canopy density (%)	93 ± 9	89 ± 9	609.0	0.0005
Number of canopy layers (1-5)	1.7 ± 0.8	1.4 ± 0.7	791.5	0.0472
Maximum canopy height (m)	5.9 ± 1.9	4.3 ± 1.9	505.0	0.0000
Litter cover (%)	82.0 ± 22.4	64.5 ± 26.3	477.5	0.0000
Litter depth (cm)	5.8 ± 1.7	5.4 ± 2.7	833.0	0.0985
Distance to nearest conspecific adult (cm)	143 ± 72	289 ± 190	553.5	0.0001
dbh of nearest conspecific adult (mm)	78 ± 41	190 ± 116	536.0	0.0000
Distance to nearest heterospecific adult (cm)	77.6 ± 38	61.2 ± 33	809.0	0.0655

Table

Species occurrence	Whole model		Explanatory variables			
	AIC	p	Factor	Influence	Wald \tilde{Q} χ^2	p
<i>Q. faginea</i>	88.4	0.0000	Canopy height	+	7.43	0.006
			Litter cover	+	9.61	0.002
			dbhNCA	-	9.55	0.002
			DNHA	+	4.47	0.035

Table

	Whole model		Explanatory variables			
	AIC	<i>p</i>	Factor	Influence	Wald \tilde{Q} χ^2	<i>p</i>
<i>Q. faginea</i>	94.5	0.0000	Canopy layers	+	11.75	0.0006
			Canopy density	-	5.09	0.0241
			DNCA	+	6.62	0.0101
			Litter depth	+	11.98	0.0005
			Qc/Vt NA	-	37.92	0.0000
<i>Q. suber</i>	98.5	0.0000	DNCA	+	46.29	0.0000
			Litter cover	+	10.46	0.0012
			Litter depth	-	12.71	0.0004

Figure
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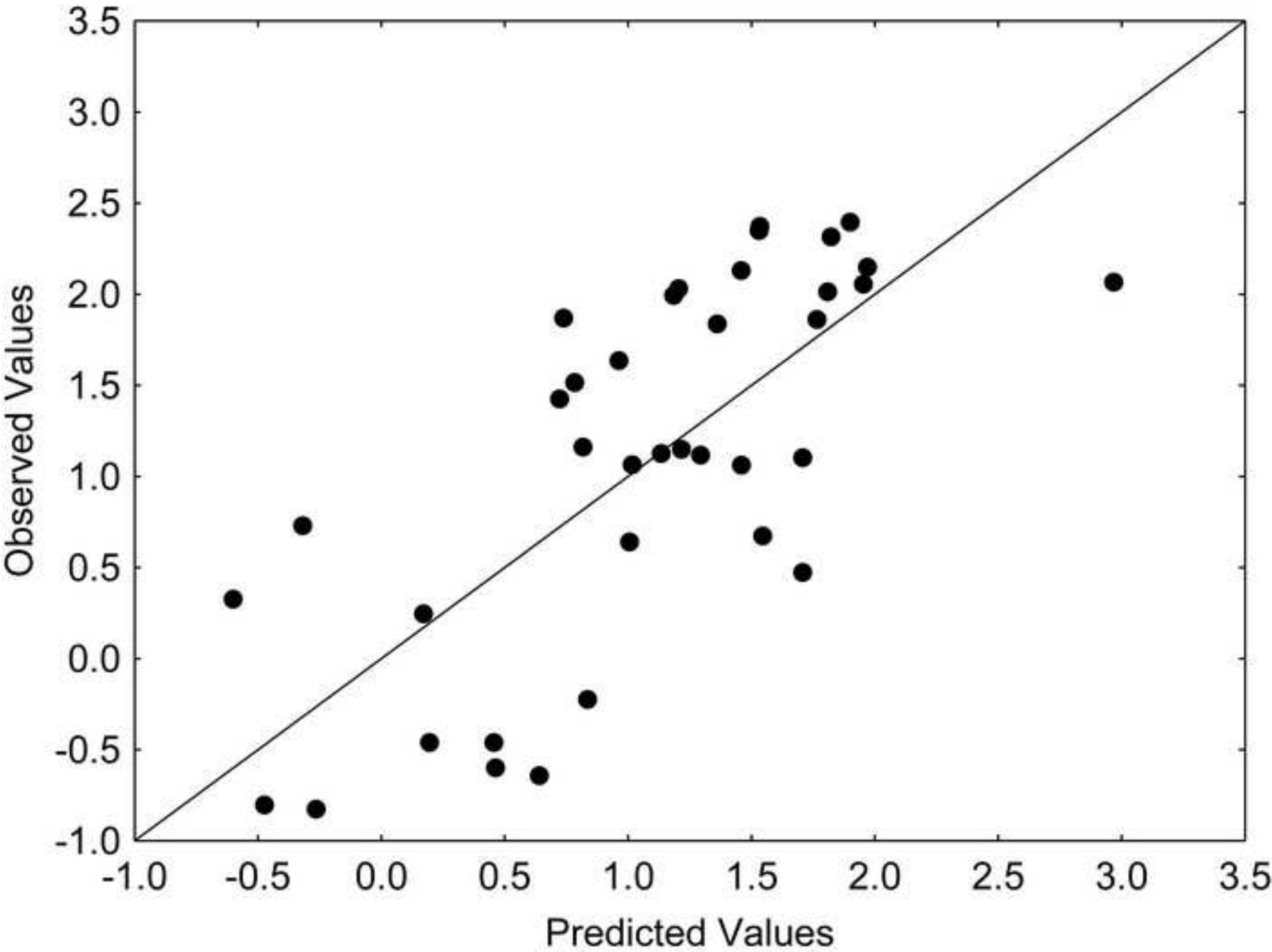
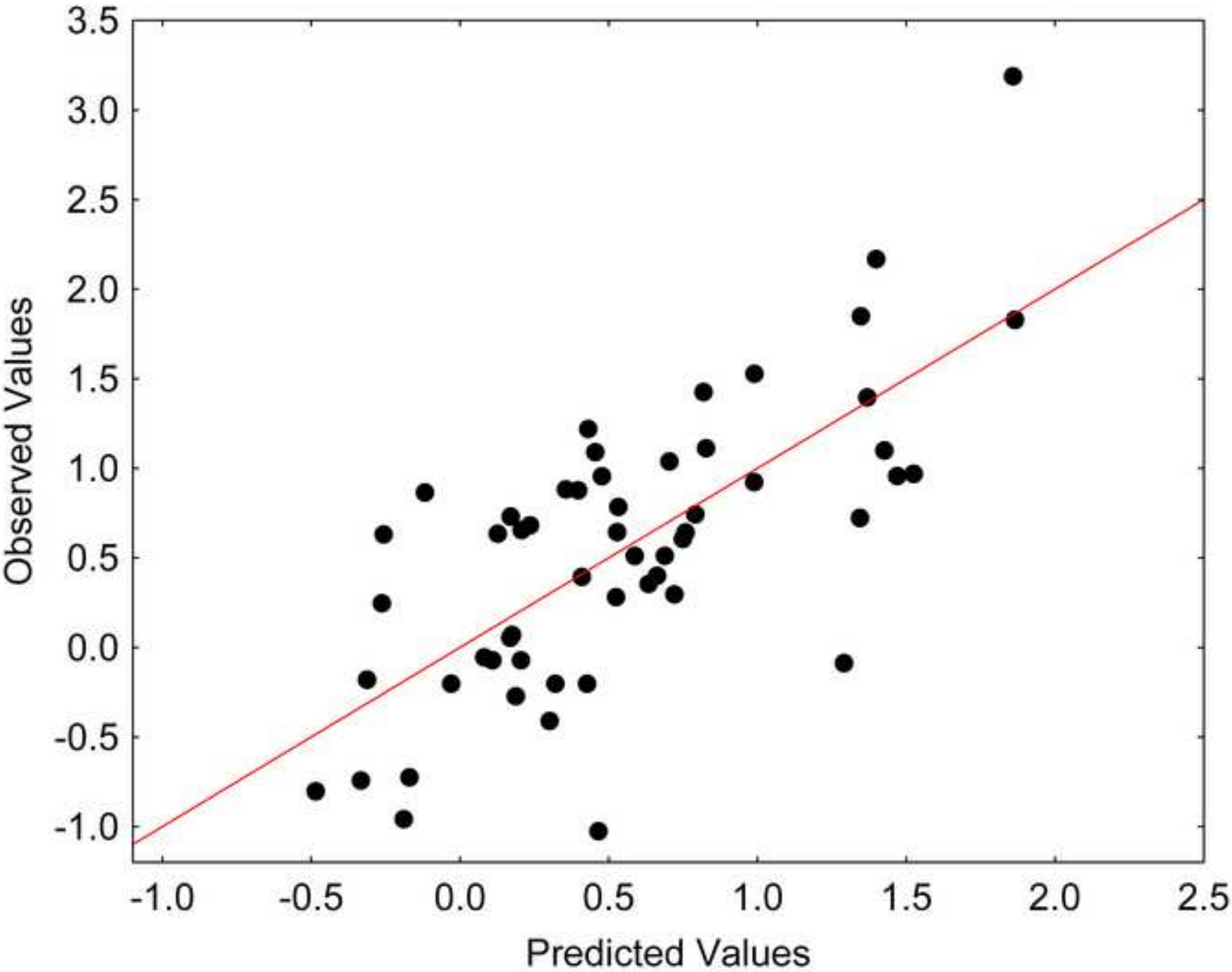
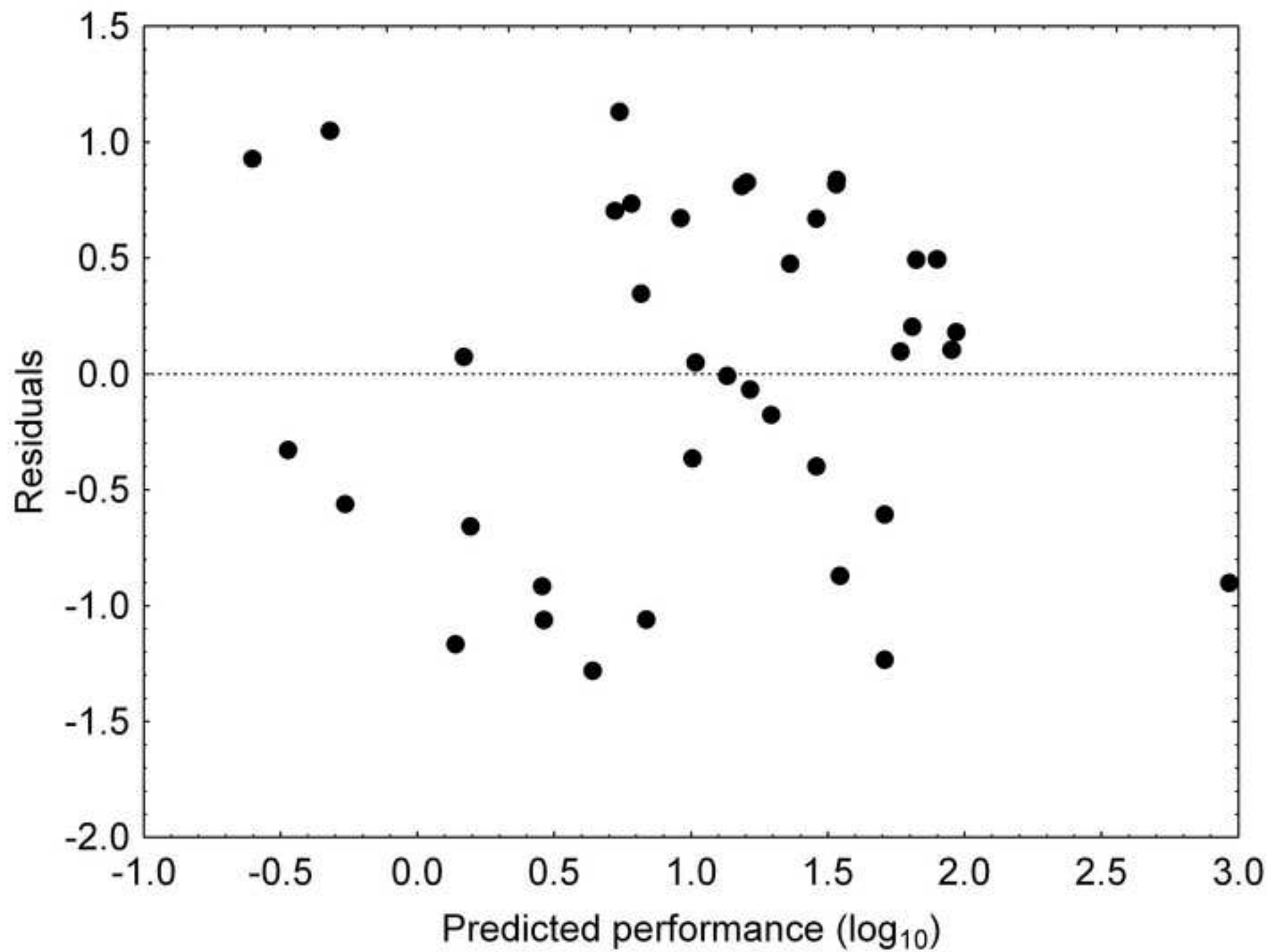


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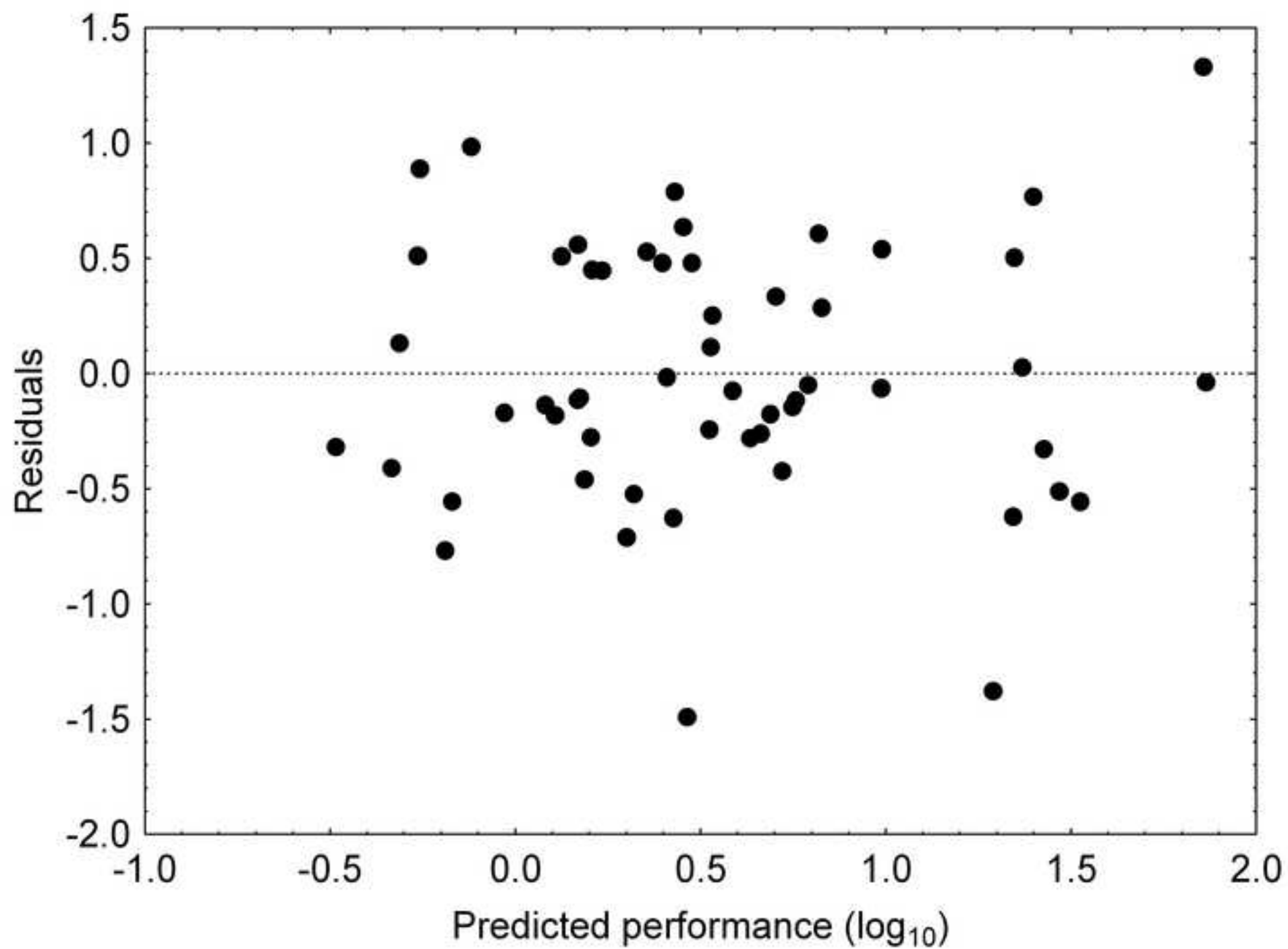
Figure

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